

2017-07-01

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Brown, Thomas

<http://hdl.handle.net/10026.1/9862>

10.1093/plankt/fbx030

Journal of Plankton Research

Oxford University Press (OUP)

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Transfer of ice algae carbon to ice-associated amphipods in the high-Arctic pack ice environment

Thomas A. Brown^{1,2*}, Philipp Assmy³, Haakon Hop^{3,4}, Anette Wold³ and Simon T. Belt²

¹ Marine Ecology and Chemistry, Scottish Association for Marine Science, Oban, Argyll,
UK, PA37 1QA.

² School of Geography, Earth and Environmental Sciences, University of Plymouth,
Plymouth PL4 8AA, UK

³ Norwegian Polar Institute, Fram Centre, N-9296 Tromsø, Norway

⁴ Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and
Economics, UiT The Arctic University of Norway, N-9037 Tromsø, Norway

* Corresponding author: Thomas.Brown@sams.ac.uk

ABSTRACT

Sympagic (ice-associated) amphipods channel carbon into the marine ecosystem. With Arctic sea ice extent in decline, it is becoming increasingly important to quantify this transfer of sympagic energy. Recently, a method for quantifying sympagic particulate organic carbon (iPOC) in filtered water samples was proposed based on the abundances of the Arctic sea ice biomarker IP₂₅. Here, we tested the hypothesis that adoption of this method could also provide quantitative estimates of iPOC transfer within Arctic amphipods. We analysed five amphipod species collected north of Svalbard and compared findings to some previous studies. Estimates showed that *Onisimus glacialis* and *Apherusa glacialis* contained the most iPOC, relative to dry mass (23.5 ± 4.5 and 9.8 ± 1.9 mg C g⁻¹, respectively), while *Gammarus wilkitzkii* had the highest grazing impact on the available ice algae (0.48 mg C m⁻², for an estimated 24 h), equating to 73% of algal standing stock. Our findings are also broadly consistent with those obtained by applying the H-Print biomarker approach to the same samples. The ability to obtain realistic quantitative estimates of iPOC into sympagic and pelagic fauna will likely have important implications for modelling energy flow in Arctic food webs during future climate scenarios.

KEYWORDS: Arctic amphipods, organic carbon, IP₂₅, H-Print, Nansen Basin

INTRODUCTION

Arctic sea ice provides a unique habitat for ice-associated algae, in particular diatoms (Dieckmann and Hellmer, 2010; Leu *et al.*, 2015), which offer food for a wide range of heterotrophic organisms, with some of the most noticeable being certain crustaceans (Arrigo, 2014) such as copepods, decapods, euphausiids and amphipods (Arndt and Swadling, 2006). In Arctic waters, analyses of baited traps and sediment traps have demonstrated that amphipods can dominate biomass in such settings (Nygård *et al.*, 2009; Kraft *et al.*, 2010) and so, in turn, provide an important link between sea ice algae and intermediary, as well as higher trophic level consumers, including fish, seabirds and marine mammals (Lønne and Gabrielsen, 1992; Lønne and Gulliksen, 1989; Dalpadado *et al.*, 2016). With Arctic sea ice extent receding (Serreze *et al.*, 2016), there is a growing need to understand the impact of potential changes in the timing, magnitude and composition of ice algal blooms and the consequences for sympagic, pelagic and benthic grazers (Søreide *et al.*, 2013; Leu *et al.*, 2015), since ice-associated amphipods are particularly sensitive to changes in sea ice conditions related to climate change (Kraft *et al.*, 2010; Barber *et al.*, 2015).

The direct coupling between sympagic (i.e. sea ice associated) and pelagic communities has been demonstrated recently following the identification of the Arctic sea ice diatom biomarker IP₂₅ (Fig. 1; Belt *et al.*, 2007) in ice-associated zooplankton during springtime (Brown and Belt, 2012a). IP₂₅ is a highly branched isoprenoid (HBI) lipid that serves as a selective tracer of ice-derived organic matter since it is only biosynthesized by certain Arctic sympagic diatoms (Belt *et al.*, 2007; Brown *et al.*, 2014c). Although these particular diatoms are generally the minority species, they are, nonetheless, pan-Arctic in distribution (Brown *et al.*, 2014c). The presence and abundance of IP₂₅ in Arctic sea ice correlate well with spring sea ice diatom biomass (Brown *et al.*, 2011), which has led to the use of this lipid as a qualitative biomarker for sea ice particulate organic carbon (iPOC)

(Brown *et al.*, 2016). Consistent with this, IP₂₅ has been identified in sinking iPOC (Belt *et al.*, 2008; Brown, 2011; Brown *et al.*, 2016), sediments (Belt and Müller, 2013) and animals (Brown *et al.*, 2014a, 2015; Brown and Belt, 2012b) across the Arctic.

In a previous case study investigation, the quantification of IP₂₅ in bulk zooplankton from the Amundsen Gulf (Beaufort Sea) between February and June 2008, demonstrated further that analysis of IP₂₅ represents a potentially useful method for confirming the link between ice algae and heterotrophs (Brown and Belt, 2012a). During the sampling period, increases in the grazing impact of zooplankton were inferred based on higher IP₂₅ concentrations within zooplankton, signifying an increase in ice algal grazing. However, a more thorough understanding of the effects of declining sea ice thickness and extent, and therefore sympagic algae, on Arctic animals requires more detailed quantification of sympagic carbon consumption, which, until recently, has not been achievable from IP₂₅ concentration data alone. However, a more recent study demonstrated that concentrations of IP₂₅ measured in seawater beneath sea ice during the spring melt can be used to obtain quantitative estimates of sinking iPOC (Brown *et al.*, 2016). In essence, quantitative estimates of iPOC in the water column were obtained by combining respective IP₂₅ concentrations with the iPOC/IP₂₅ ratio derived from analysis of the overlying sea ice. Using this approach, Brown *et al.* (2016) showed that iPOC accounted for up to 100% of the total organic carbon available to consumers in the upper water column at the time when sympagic algae were being released from the ice matrix.

Combined, the previous identification of IP₂₅ in zooplankton (Brown and Belt, 2012a) and the recent demonstration that iPOC could be quantified in the water column (Brown *et al.*, 2016), led us to hypothesise that a similar approach could be used to quantify iPOC in Arctic primary consumers, such as some amphipod species that are known to graze on ice algae. Here, we tested this hypothesis by 1) determining the iPOC/IP₂₅ ratio within ice algal

aggregates collected beneath sea ice, north of Svalbard in the Nansen Basin, 2) quantifying IP₂₅ in amphipods sampled from beneath sea ice that were observed feeding on ice algae, and 3) combining these findings to quantify iPOC in amphipods. Having established a means of quantifying iPOC in amphipods, our aim was to provide the first quantitative estimates of iPOC consumption for *in-situ* ‘autochthonous’ (permanently inhabiting sea ice) amphipod species; *Gammarus wilkitzkii* Fabricius, 1775, *Apherusa glacialis* Hansen, 1887, *Onisimus nansenii* Sars, 1900, *Onisimus glacialis* Sars, 1900 and the ‘allochthonous’ (partly ice-associated) amphipod, *Eusirus holmi* Hansen, 1887. To complement the iPOC/IP₂₅ approach, we also calculated the so-called H-Print (Brown *et al.*, 2014d; Brown and Belt, 2017) for each sample, a method that combines the relative abundances of a variety of diatom-derived HBIs, and has been adopted previously to provide semi-quantitative estimates of the proportion of sympagic versus pelagic carbon in zooplankton (Brown and Belt, 2017) fish, seals and marine mammals (Brown *et al.*, 2017).

METHOD

Site description and sample collections

The area of sample collection was in the Nansen Basin north of Nordaustlandet, Svalbard (Fig. 2). Ice algal aggregates and ice-associated amphipods were collected at an ice-station during the ICE12 expedition in July 2012, where the Norwegian Polar Institute research vessel *Lance* was moored to a large drifting ice floe at starting point 82.5°N, 21°E. The drift was southward towards the outer margins of the marginal ice zone (Fig. 2). The sea ice comprised mainly first-year ice and extended over a region where the water depth was up to 2500 m.

Sampling of ice algal aggregates

Floating ice algal aggregates were collected with a coarse-meshed sieve through a specially drilled ice hole (3.2 m² in size) at 12 h intervals from 29 July – 1 August 2012 (for more details see Assmy *et al.*, 2013). Upon return to the ship, ice algal aggregates were transferred into 50 mL centrifuge tubes and frozen at -20°C.

Sampling of amphipods

Samples of amphipods were collected on 24 separate occasions from 28 July – 1 August 2012 below the ice by scuba divers using an electrical suction pump with a 500 µm mesh net (Lønne, 1988). Qualitative sampling of amphipods for IP₂₅ analysis was carried out by sampling as many organisms as possible during 40–60 min of diving. The amphipods were sorted by species and frozen at -80 °C in zip-lock plastic bags.

Quantitative amphipod sampling was carried out by scuba divers using 50 × 50 cm standard frames (Hop *et al.*, 2000). Electrical suction pumps were used to collect samples from a set area of flat or ridged sea ice by placing these frames 10 times (one replicate sample) in a direction from the dive hole where ice amphipods occurred and exhaled bubbles were absent. Replicates (5 per flat or ridged sea ice) were taken by a single diver in different directions from the dive hole to avoid repeated sampling of the same under-ice area. The samples were preserved in buffered formaldehyde solution at a final concentration of 4% and were subsequently analysed for species composition, abundance and biomass at the Institute of Oceanology, Sopot, Poland. The total length of amphipods was determined from formaldehyde-preserved organisms blotted on filter paper. Abundance estimates (per m²) were made based on the area covered for each replicate sample (2.5 m²).

Total organic carbon

Sub-samples (~50 mg) of freeze-dried algae were decarbonated (10% HCl; 10 mL), washed (3 × 10 mL Milli-Q water) and freeze-dried prior to analysis using a Thermoquest EA1110 CHN analyser. L-cystine was used as a calibration standard.

Lipid extraction and purification

Extraction of HBI lipids from freeze-dried algae and amphipods was carried out using established techniques (Belt *et al.*, 2012; Brown *et al.*, 2014d). An internal standard (9-octylheptadec-8-ene (9-OHD); 10 µL; 2 µg mL⁻¹) was added to enable the quantification of IP₂₅ (Belt *et al.*, 2012). Samples were covered in methanol (4 mL) and amphipods were mechanically crushed using a glass rod. Samples were then sonicated for 10 min. Milli-Q water (1 mL) and hexane (3×4 mL) were added, and then solutions were vortexed (1 min) and centrifuged (2 min; 2500 revolutions min⁻¹). Supernatant solutions containing lipids were transferred to clean vials with glass pipettes and dried (N₂ stream). Extracts were then re-suspended in hexane (1 mL) and fractionated, providing non-polar lipids (IP₂₅ and other HBIs) using column chromatography (5 mL hexane; SiO₂; 0.5 g).

Lipid analysis

Analyses of purified non-polar lipid extracts containing IP₂₅ and other HBIs were carried out using gas chromatography–mass spectrometry (GC–MS) (Belt *et al.*, 2012). Total ion current (TIC) chromatograms were used to determine the retention times and mass spectra of HBIs, and these were compared with those of authentic standards (Belt *et al.* 2012) and published literature (Brown 2011 and references therein) for identification purposes.

HBI quantification

For gravimetric quantification of IP₂₅, GC–MS responses were obtained in selective ion monitoring (SIM) mode (m/z 350.3) and were normalised using instrumental response factors and the masses of internal standard and sample mass (Belt *et al.*, 2012).

iPOC quantification

Based on a previous method for estimating iPOC in seawater (Brown *et al.*, 2016), range and mean estimates of the iPOC content of amphipods (iPOC_{amph}) were obtained by combining amphipod IP₂₅ concentrations with iPOC/IP₂₅ ratios derived from an ice algal aggregate sampled on 29 June 2012 (Eq. 1). iPOC_{amph} concentration estimates were obtained for the five amphipod species sampled.

(1)

$$iPOC_{amph} = IP_{25} \text{ (amphipod)} \times \frac{iPOC_{(aggregate)}}{IP_{25} \text{ (aggregate)}}$$

HBI biomarker H-Print

H-Prints (%) were calculated using the abundance of pelagic (III) and sympagic (IP₂₅ and II) HBIs according to Eq. 2.

(2)

$$H - Print \% = \frac{(III)}{(IP_{25} + II + III)} \times 100$$

In addition to quantifying sympagic carbon contribution to amphipod diet using equation 1, estimates of the proportion of sympagic carbon (with 99% confidence intervals), relative to total marine carbon (i.e. sympagic plus pelagic), were also derived by converting H-Prints using a previously modelled regression curve (Brown and Belt, 2017).

Statistical analysis

Statistical analysis was carried out in R-Studio version 1.0.136 (R-Core-Team, 2016). ANOVA, with post-hoc Least Significant Difference mean separation tests (pairwise comparisons), was used to compare iPOC_{amph} between amphipod species. A student’s t-test for two samples was used to compare iPOC_{amph} between different size groups of the same species. All data are reported as mean \pm standard error unless stated otherwise with tests considered significant at $\alpha = 0.05$.

RESULTS

Ice algae aggregates

Taxonomic analysis of floating ice algal aggregates (1–15 cm in diameter) sampled within the meltwater layer during the ICE12 cruise showed an assemblage of densely packed diatoms, with a dominance of the ice-associated pennate diatoms *Navicula pelagica*, *Hantzschia weyprechtii*, *Entomoneis paludosa* and *Cylindrotheca closterium* (Assmy *et al.*, 2013). Our analysis of one of these ice algal aggregates, which was sampled alongside amphipods, showed a total organic carbon (TOC) content (261 ± 5 mg g⁻¹; 26%) consistent with previous data from diatom cultures (e.g. *Berkeleya rutilans* 30%; Brown *et al.*, 2014b) and floating ice algal aggregates (27–31%; Brown *et al.*, 2014c). The IP₂₅ content was 1.14 ± 0.02 μ g g⁻¹, giving an iPOC/IP₂₅ ratio of $2.29 \pm 0.04 \times 10^5$; $n = 6$. The dominance of sea ice diatom species within the aggregate was also reflected in the H-Print (<1%; $n = 5$).

iPOC in amphipods

The mean abundance of the individual species, derived from 24 separate sampling operations (Table 1, Fig. 3), showed that *Apherusa glacialis* (mean 7.7 ind. m⁻²) and *Onisimus nanseni*

(0.1 ind. m⁻²) were the most and least abundant species, respectively. The largest species, *Gammarus wilkitzkii*, was the second most abundant (0.7 ind. m⁻²), while *Eusirus holmi* and *Onisimus glacialis* were comparable (0.3 ind. m⁻²).

Our iPOC_{amph} estimates show that *G. wilkitzkii* contained the most iPOC, with between 96 and 2052 µg C ind⁻¹ for specimens ranging in length from 15–40 mm (Fig. 4a-b). Such specimens contained significantly more iPOC_{amph} than any other species, including *E. holmi*, despite being of similar size ($F = 15.8$, $df = 4$, $p = <0.001$; Table 1). In general, larger individuals of *G. wilkitzkii* (>35 mm) had ca. 4 times more iPOC_{amph} than smaller specimens (<20 mm) ($t = 2.8$, $df = 9.3$, $p = 0.02$). Normalisation of iPOC_{amph} estimates to account for amphipod mass (dry) revealed that *O. glacialis* had the highest dry mass (DM) normalised iPOC_{amph}, with more than twice as much iPOC_{amph} as any other species ($F = 13.6$, $df = 4$, $p = <0.001$; Table 1). In contrast to absolute iPOC_{amph} estimates, the DM normalised iPOC_{amph} content of *G. wilkitzkii* was similar to the much smaller *A. glacialis* ($F = 13.6$, $df = 4$, $p = <0.001$). Finally, DM normalised data revealed that *E. holmi* and *O. nansenii* had similar iPOC_{amph} content, both being significantly less than other species (Table 1), despite their difference in size (28±1.5 mm and 14±4 mm respectively).

The quantity of iPOC_{amph} per unit area of sea ice at the time of sampling was estimated by combining mean iPOC_{amph} values with mean amphipod abundance derived from the 24 separate observations made during sampling. This showed that the amount of iPOC being retained by amphipods was ca. 0.66 mg iPOC m⁻² (Table 1). The majority of iPOC_{amph} was found within *G. wilkitzkii* (73%; 0.48 mg m⁻²), followed by *A. glacialis* (19%), with *O. glacialis*, *E. holmi* and *O. nansenii* containing the least (all <5%; 0.03 mg m⁻²). When compared to the carbon standing stock of ice algal aggregates (0.74 mg C m⁻²; from Assmy *et al.* (2013)), iPOC_{amph} in the five amphipod species corresponded to approximately 89% of available ice algal aggregate carbon.

Source of amphipod POC

The majority (95%) of amphipod H-Prints for all species ranged from 0.1 to 7.2% (Fig. 4g-h), with only four individuals (all *A. glacialis*) having H-Prints >7.2% (12.0, 13.1, 40.1 and 62.2%). Using the regression model defined previously by Brown and Belt (2017), these H-Print values were re-expressed to estimate % sympagic carbon consumed by amphipods. In all cases, mean % sympagic consumption was estimated as >90% (Table 1).

DISCUSSION

Organic carbon and IP₂₅ content of sea ice algal aggregate

The iPOC/IP₂₅ ratio used in the current study ($2.29 \pm 0.04 \times 10^5$) is much higher than that reported previously for sea ice POC from Resolute Bay in the Canadian Arctic (ca. 2.6×10^3 ; Brown *et al.*, 2016) and we provide two explanations for this. Firstly, in contrast to the Resolute Bay sea ice samples, there were high amounts of extracellular polymeric substances (EPS) in the ICE12 sea ice algal aggregates from the Arctic Ocean (Assmy *et al.*, 2013), consistent with a ‘stressed/old’ community (Søreide *et al.*, 2006), and supported further by observations of a large number of empty diatom frustules (Assmy *et al.*, 2013). In addition, the percentage of IP₂₅-producing species in the ICE12 algae was lower (<0.1%) compared to Resolute Bay (0.3–3.6%; Brown *et al.*, 2014c). Since ICE12 aggregates were sampled from within the water column, rather than directly from within sea ice, this reduction could potentially be due to the *in-situ* incorporation of non-IP₂₅ producing phytoplanktic species, although Assmy *et al.* (2013) showed that the aggregate composition was dominated by ice-associated diatoms and this is supported here by very low H-Prints (<1%). Instead, although *Haslea crucigeroides*, a known producer of IP₂₅ (Brown *et al.*, 2014c), could be identified in the ICE12 aggregates (T. A. Brown, pers. obs.), it was not sufficiently abundant to be

included in previous taxonomical reports (Assmy *et al.*, 2013). Indeed, the IP₂₅-producing species (*H. crucigeroides*, *H. spicula*, *H. kjellmanii* and *Pleurosigma stuxbergii* var *rhomboides*) are typically <1% of sea ice diatom assemblages from north-east Svalbard and west Greenland (von Quillfeldt, 2000), while the same species comprised >3% of the diatoms present in the Resolute Bay aggregates (Brown *et al.*, 2014c and references therein). In any case, regardless of the exact reasons for the differences in iPOC/IP₂₅, this study reinforces the importance of measuring this ratio on a case-by-case basis, as recommended by Brown *et al.* (2016). In contrast, adoption of a fixed value for iPOC/IP₂₅ will likely lead to anomalous estimates of iPOC within suspended/sinking POC and food-web constituents, as discussed in detail by Brown *et al.* (2016).

Quantitative estimates of ice-derived organic carbon in amphipods

IP₂₅ was present in each of the amphipod specimens analysed, enabling us to estimate iPOC_{amph} in all cases. iPOC_{amph} estimates varied by three orders of magnitude, broadly reflecting the range in amphipod size, with the smallest (*A. glacialis*) and largest (*G. wilkitzkii*) containing the lowest and highest iPOC_{amph}, respectively. Dry mass-normalised abundances showed the opposite trend, however, with smaller species (and smaller individuals of species) having relatively higher iPOC_{amph}, which aligns with smaller animals having to sustain higher weight-specific ingestion rates to offset their higher metabolic activity (c.f. larger animals) (Werner, 1997). On the other hand, this size-dependant difference in iPOC_{amph} may potentially reflect the variable dietary preference of amphipods, especially as the smaller *A. glacialis* are more herbivorous than the larger and mainly omnivorous/carnivorous *G. wilkitzkii* (Poltermann, 2001).

Next, by expressing the iPOC_{amph} values as a percentage of estimated amphipod carbon content (ca. 40%; Werner, 1997; Yuichiro and Tsutomu, 2003; Kiørboe, 2013; Fig

5e–f), our data show that <13% of amphipod body carbon comprised carbon derived from sea ice algal aggregates, in good agreement with data obtained from captive *G. wilkitzkii*, *O. nansenii* and *A. glacialis*, which consumed between 0.1 and 16% of body carbon during experiments carried out in fixed-volume vessels containing physical ice substrate (Werner, 1997).

We then combined iPOC_{amph} data with the TOC content of ICE12 aggregates to obtain estimates of the total mass of ice algae consumed by amphipods. Our data indicate that individual *G. wilkitzkii* had consumed between 0.5 and 5 mg of ice algal aggregate leading up to their capture during our sampling campaign. Since our data represent *in-situ* values, it is not possible to definitively report data as estimates of daily consumption rates that would facilitate direct comparisons with other studies. However, comparison of our iPOC_{amph} estimates to consumption rates reported previously for *Gammarus* spp. feeding on macrophytes in the Baltic Sea (1–5 mg ind. d⁻¹; Orav-Kotta *et al.*, 2009) and captive *G. wilkitzkii* (0.08–0.14 mg algae ind. d⁻¹; Werner, 1997), indicate that our estimates likely also reflect grazing rates over approximately 24 h. Further direct comparisons of iPOC/IP₂₅ derived values between *in-situ* and captive zooplankters might improve such comparisons in the future.

Finally, by combining iPOC_{amph} with amphipod abundance (i.e. number of individuals per unit area) for each of the five species, we estimate that iPOC_{amph} accounted for ca. 89% of the available ice algal aggregate carbon during the course of sampling, which agrees well with previous estimates of 63% and 58–92% (Siferd *et al.*, 1997; Kohlbach *et al.*, 2016). Similarly, our consistent amphipod H-Prints indicate that most amphipod species appeared to be obtaining energy almost exclusively (>90%; Table 1) from ice algal aggregates. On the other hand, based on a composite of field-measured abundances and laboratory-based grazing studies, Werner (1997) estimated the daily grazing impacts of *A. glacialis*, *Onisimus* spp. and

G. wilkitzkii to be ca. 1.1 and 2.6% for the Laptev and Greenland Sea, respectively. One explanation for these different outcomes might be associated with the high degree of variability in amphipod abundance, which is strongly seasonally dependent in response to the development of sea ice (Siferd *et al.*, 1997; Werner and Auel, 2005). Thus, it is possible that our amphipod abundances (and therefore estimates of grazing impact) were influenced, to some extent, by the sea ice conditions during the late melt season, when the sea ice was becoming increasingly heterogeneous, with a growing number of melt ponds (Assmy *et al.*, 2013). At this time in the season, after much of the iPOC had likely already been exported (e.g. Brown *et al.*, 2016), it is also possible that ice algae aggregates represented an important and concentrated food source in an otherwise relatively oligotrophic period. In this case, amphipod diet at the time of sampling would likely be dominated by ice algae, rather than other sources, resulting in relatively high estimates of grazing impact.

A part of iPOC_{amph} could have been acquired from other carbon sources since, for example, large *G. wilkitzkii* has an omnivorous diet, and consumes both zooplankton and ice amphipods (Werner, 1997; Søreide *et al.*, 2006). The most likely candidates of zooplankton prey is *Calanus glacialis*, which is known to utilize ice algal blooms to fuel early maturation and reproduction (Søreide *et al.*, 2010). Qualitative assessment of herbivory/carnivory in amphipods has been established based on faecal pellet colouration, where green-yellow and orange-red pigments indicate herbivory and carnivory, respectively (Werner, 2000). Accordingly, the observed orange colouration of *G. wilkitzkii* lipid extracts in this study likely indicates that this species incorporated at least some of the estimated iPOC_{amph} through carnivory, likely from *Calanus* sp., rather than direct herbivory. Despite this, we note that our *G. wilkitzkii* iPOC_{amph} data remain comparable to other captive grazing experiments where carnivory was absent (Fig. 4 d,f; Werner, 1997). Indeed, it is well established that IP₂₅ is transferred across trophic levels, and is readily identified in Arctic consumers, from fish

(Brown and Belt, 2012b; Brown *et al.*, 2015) and seabirds (Megson *et al.*, 2014), right up to marine mammals (Brown *et al.*, 2013, 2014a).

iPOC_{amph} in *Eusirus holmi*

In contrast to the other amphipod species in this study, comparison of iPOC_{amph} data with literature values was not possible for *E. holmi*, despite this species being pan-Arctic in distribution (Tencati and Geiger, 1968; Siferd, 2015). The limited reporting of *E. holmi* likely reflects its low abundance in the Arctic, rather than difficulties in identification, as it is easily recognized based on its light orange eyes, orange markings on coxa and pleopods, and four long antennae and long leg segments. *Eusirus holmi* accounted for ca. 3% of the amphipods in our samples and was even lower (<1%) in a previous study from the same region (Macnaughton *et al.*, 2007). Our iPOC_{amph} data therefore likely represent the only documented estimates of iPOC consumption for this species. Notably, absolute iPOC_{amph} estimates in *E. holmi* were most similar to those for the smaller *A. glacialis* and *O. nanseni*, while normalised (dry body mass) values were also comparable to the much smaller *O. nanseni*. Although the paucity of literature data prevents us from assessing our iPOC_{amph} estimate for *E. holmi* further, we note that, in contrast to the other species investigated here, a relatively low iPOC_{amph} content for this species might imply that it obtained the majority of its organic carbon from sources other than sea ice algae. *Eusirus holmi* is frequently observed by divers in the water column, typically with legs spread out to suspend itself while slowly sinking. It occasionally propels itself upwards with its large telson and then repeats the slow sinking. This likely represents the feeding behaviour of *E. holmi* in the water column, but it can also be observed clinging to the underside of sea ice. However, the consistent H-Print values indicated that ca. 100% (86-115%; 99% CI) of marine carbon in amphipods was of sympagic origin (Table 1). While there are a number of potential reasons for the low

iPOC_{amph} estimates, including, for example, selectivity during grazing, further analysis of this species will be necessary before firmer conclusions can be made. What is clear, however, is that the low field abundances of *E. holmi* in other studies and low iPOC_{amph} content estimated here indicate that this species is currently of minor importance with respect to channelling the sympagic carbon component into the ecosystem, at least in comparison to other more abundant species in this study, particularly, *G. wilkitzkii* and *A. glacialis*.

Having focused here on a somewhat localised setting, we anticipate that further application of this technique to a wider range of Arctic ice fauna and zooplankters has the potential to improve our knowledge and understanding of the role that ice algae play in supporting the broader Arctic ecosystem. Concomitant with the long-term trend of decreasing sea ice extent and thickness (Barber *et al.*, 2015), a similar decline in ice-amphipods, particularly *G. wilkitzkii* has occurred, with associated reduction of high-energy food to upper trophic consumers (Hop *et al.*, 2013). Reduction in sea ice extent in Antarctica has similarly been identified as one of the causes of the recent decline in Antarctic krill populations in the Southern Ocean (Flores *et al.*, 2012), with impacts on higher trophic level animals (Reiss *et al.*, 2017). In both polar areas, increased ridging in thinner ice may partly compensate for loss in sea ice extent by creating complex structures as enhanced habitat for sympagic fauna (Gradinger *et al.*, 2010; Melbourne-Thomas *et al.*, 2016). The more pelagic *E. holmi* may increase in abundance with changing ice conditions towards thinner first-year ice and more frequent open water in the Arctic Ocean. Under such a scenario, *E. holmi* may potentially represent an alternative energy source to that currently derived from ice algae (and associated amphipods) and, therefore, an important target for future research efforts. In any case, the data generated from this, and subsequent studies, will provide the necessary numerical input required to assist models in predicting the potential impact of declining Arctic sea ice extent

on sea ice biota, and further evaluation of sea ice algae as an energy source for other Arctic consumers.

CONCLUSION

Our data provide evidence to support our initial hypothesis that combining sea ice-derived iPOC/IP₂₅ data with IP₂₅ concentration data obtained from amphipods can provide realistic estimates of the amount of sympagic organic carbon within these primary consumers. Accordingly, we present quantitative estimates of iPOC for ice-associated amphipods and the first documented assessment of the sympagic carbon content of the understudied *E. holmi*. Our findings are also supported by data obtained from the same samples using a combined biomarker approach (H-Print). The data generated from this, and subsequent studies, will provide numerical input required to assist models in predicting the potential impact of declining Arctic sea ice extent on sea ice biota, and to further evaluate sea ice algae as an energy source for other Arctic consumers.

ACKNOWLEDGEMENTS

We are indebted to the captain and crew of RV *Lance*. We are also grateful to A Tonkin (University of Plymouth) for carrying out CHN analysis of algal aggregates. Taxonomic analyses were based on a contract with Institute of Oceanology, Sopot, Poland, with expertise administered by Slawomir Kwasniewski. We are also grateful to the Associate Editor and an anonymous reviewer for their helpful comments.

FUNDING

This work was supported by the award of a Research Project Grant from the Leverhulme Trust (UK). The ICE2012 cruise was funded and conducted as part of the Centre for Ice, Climate and Ecosystems (ICE) at the Norwegian Polar Institute.

416 Table 1. Mean (\pm se) and relative (%) amphipod abundance, ice-derived particulate organic carbon (iPOC_{amph}) and H-Print estimates (99% CI)
 417 of sympagic carbon, as a percentage of sympagic and pelagic marine carbon consumed, based on the regression model of Brown and Belt
 418 (2017).

Species	Abundance			iPOC _{amph}										H-Print estimates (%) of sympagic carbon				
	ind . m ⁻²	% of all species		n	µg C ind ⁻¹	% of all species	Signifi- cant differe- nce ¹	mg C g ⁻¹ DM	% of all species	Signifi- cant differe- nce ¹	iPOC % amphi- pod C	Signifi- cant differe- nce ¹	mg C m ⁻²	% of all species	Mean (99% CI)	Max (99% CI)	Min (99% CI)	Signifi- cant differe- nce ¹
<i>Apherusa glacialis</i>	367	7.7	85	15	16.3 ± 2.4	2	a	9.8 ± 1.9	21	a	2.5 ± 0.5	a	0.13	19	92 (78-106)	100 (86-115)	37 (24-52)	a
<i>Eusirus holmi</i>	12	0.3	3	14	54.7 ± 8.3	6	a	1.6 ± 0.2	3	b	0.4 ± 0.1	b	0.01	2	100 (86-115)	100 (86-115)	100 (86-115)	b
<i>Onismus nansenii</i>	6	0.1	1	13	68.5 ± 18.9	7	a	5.1 ± 1.1	11	ab	1.3 ± 0.3	ab	0.01	1	100 (86-115)	100 (86-115)	99 (84-113)	b
<i>Onismus glacialis</i>	15	0.3	3	10	107.5 ± 14.5	12	a	23.5 ± 4.5	49	c	5.9 ± 1.1	c	0.03	5	100 (86-115)	100 (86-115)	100 (86-115)	b
<i>Gammareus wilkitzkii</i>	34	0.7	8	34	673.6 ± 94.5	73	b	7.8 ± 1.3	16	a	2.0 ± 0.3	a	0.48	73	99 (84-113)	100 (86-115)	93 (79-108)	b

Total	$\frac{4}{3}$	9.1 4*	$\frac{8}{6}$	920.6*	47.8*	0.6 6*
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419 * Calculated from mean values

420 ¹ Least Significant Difference mean separation tests (pairwise comparisons), $\alpha = 0.05$

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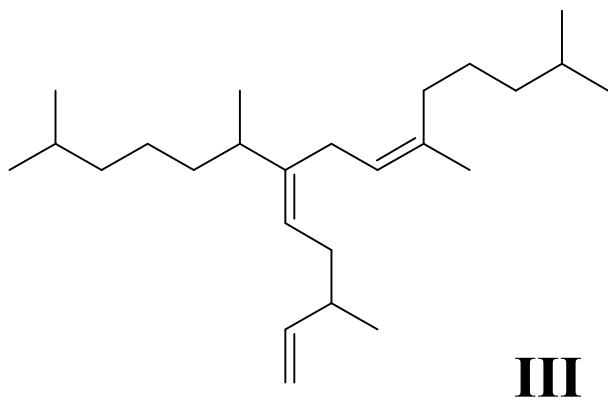
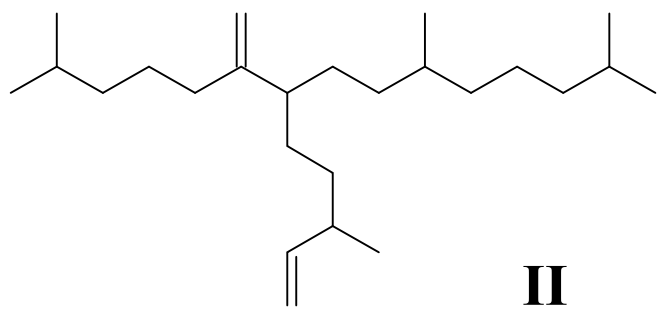
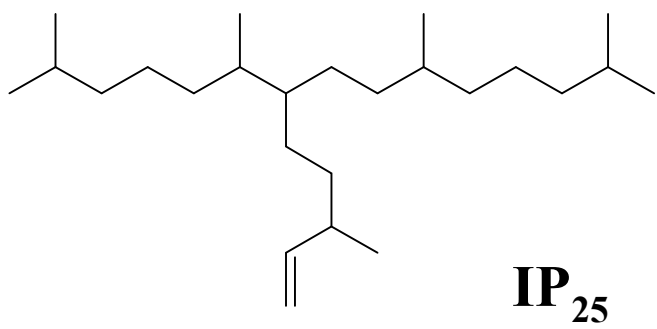
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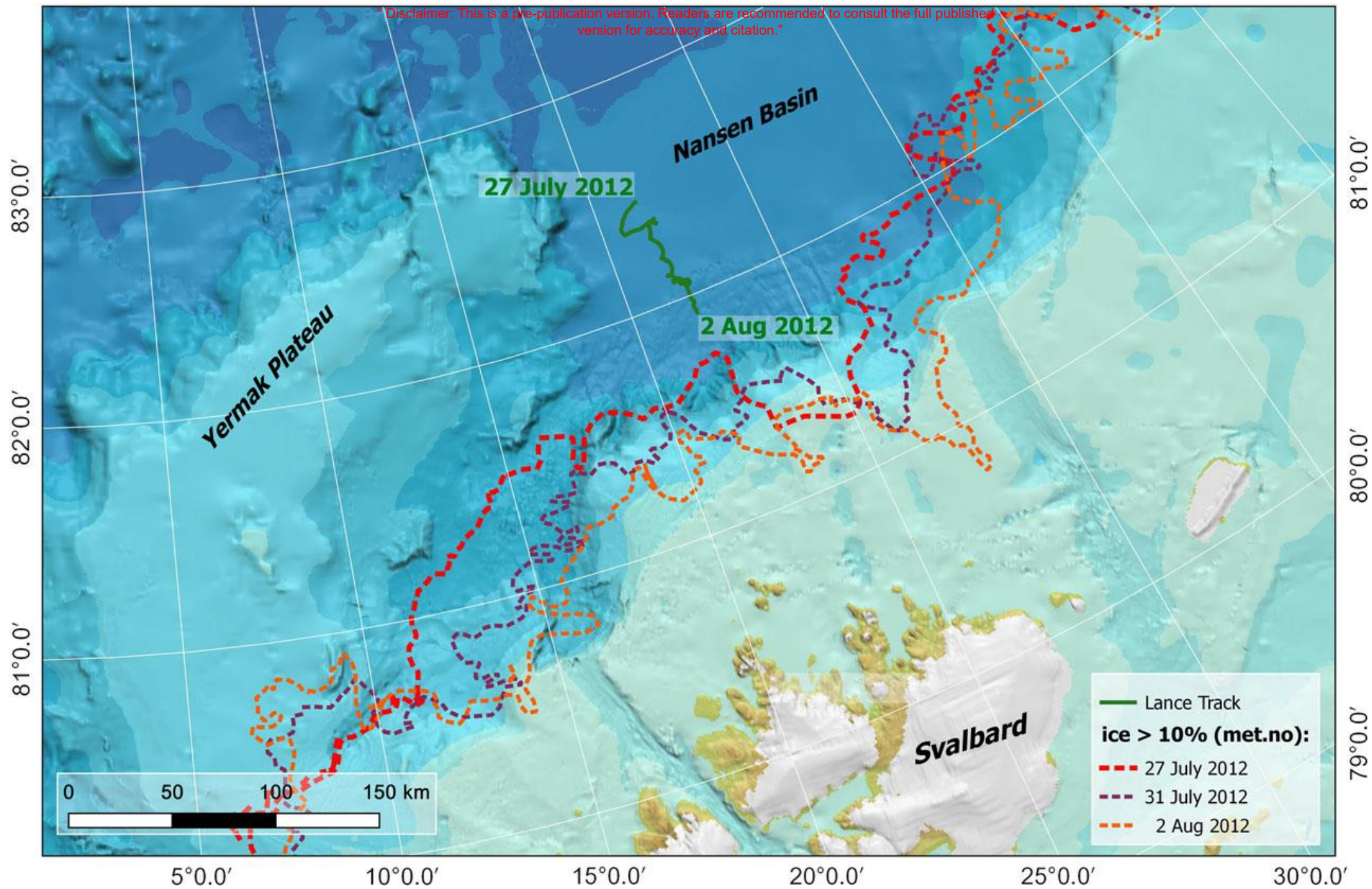
Fig. 1 Structures of sea ice diatom (IP₂₅, II) and phytoplanktic diatom (III) highly branched isoprenoids (HBIs) measured in amphipods.

Fig. 2 Study location north of Svalbard with bathymetry. Green line is the drift trajectory of the ice floe that the RV *Lance* was moored to, with start and end dates. The ice edge positions for 27, 31 July and 2 August are indicated by the broken lines and are representative for the drift period. Map created by the Norwegian Polar Institute, Max König. Bathymetry with permission from IBACO (Jakobsson *et al.*, 2012).

Fig. 3 Averaged amphipod abundance for each species beneath the ice floe during sampling (note: logged y-axis). Circles = flat under-ice surface, squares = ridged under-ice surface.

Fig. 4 Amphipod iPOC content (a-f) and H-Print (g-h; note logged scale) compared to amphipod length (left) and for species average (right). Horizontal dotted lines (a, b) represent equivalent total algal aggregate mass consumed for selected iPOC concentrations (note logged scale in b). Red dots (d and f) show data derived from laboratory experiments (Werner, 1997). Green dots (h) show the H-Print value derived from ice algal aggregates that amphipods were observed grazing upon in this study.





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